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Microsite and herbaceous vegetation heterogeneity after burning *Artemisia tridentata* steppe

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Abstract Woody vegetation can create distinct subcanopy and interspace microsites, which often result in resource islands in subcanopies compared to interspaces. This heterogeneity in soil resources contributes to herbaceous vegetation heterogeneity in plant communities. However, information detailing the impact of disturbance, such as fire, that removes the woody vegetation on microsites and herbaceous vegetation heterogeneity is limited. The purpose of this study was to determine the influence of burning on microsites and herbaceous vegetation in subcanopies and interspaces. Six study sites (blocks) were located at the Northern Great Basin Experimental Range in shrub (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh)-bunchgrass plant communities and one half of each block was burned to remove *A. tridentata*. Herbaceous vegetation and microsite characteristics were measured 2 years post-fire in intact and burned subcanopies and interspaces. Burning resulted in microsite and herbaceous vegetation differences between intact and burned subcanopies and intact and burned interspaces. However, burned subcanopies and burned interspaces appeared to be relatively similar. The similarity in microsite characteristics probably explains the lack of differences in herbaceous vegetation cover and biomass production between burned subcanopies and burned interspaces ($P > 0.05$). However, some microsite and herbaceous vegetation characteristics differed between burned subcanopies and burned interspaces. Our results suggest that disturbances that remove woody vegetation reduced microsite and herbaceous vegetation heterogeneity within plant communities, but do not completely remove the resource island effect. This suggests soil resource heterogeneity may influence post-fire community assembly and contribute to diversity maintenance.

Keywords Coexistence · Disturbance · Micro-environment · Prescribed fire · Resource island

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Introduction

Arid and semi-arid ecosystems are often characterized by high levels of bare ground interspersed by distinct patches of vegetation. These distinct patches are caused, in part, by woody species (trees and shrubs) creating resource islands under their canopies (subcanopies) compared to interspaces (Jackson and Caldwell 1993a, b). These resource islands have been documented in *Artemisia tridentata* Nutt. (big sagebrush) plant communities (Charley and West 1977; Doescher et al. 1984; Burke et al. 1987; Wight et al. 1992; Davies et al. 2007a), woodlands (Evans and Ehleringer 1994; Kaye and Hart 1998), coastal dunes (Alpert and Mooney 1996), and hot deserts (Herman et al. 1995; Schlesinger et al. 1996; Whitford et al. 1997). Woody species also may facilitate the growth of other plants under their canopies by creating micro-environments that are favorable for vegetation growth (Pierson and Wight 1991; Miller and Rose 1995; Callaway et al. 1996; Schultz et al. 1996; Chambers 2001; Davies et al. 2007a).

Many plant communities experience periodic wildfires that remove woody vegetation (Humphrey 1974; Wright and Bailey 1982). However, there is limited information on subcanopy and interspace characteristics after fire has removed the woody vegetation. Existing information suggests that inorganic N differences between subcanopies and interspaces increase initially after prescribed burning (Stubbs and Pyke 2005). Soil water repellency and erosion may also increase in subcanopies compared to interspaces after fire (Pierson et al. 2001; Ravi et al. 2007). Increased erosion in subcanopies after fire may result in redistribution of soil particles and nutrients, and thus, potentially decrease resource island effects (Ravi et al. 2007). To better understand the functional relationships in plant communities with woody vegetation, information detailing the impact of fire on microsite and herbaceous vegetation heterogeneity is needed. The impacts of fire on the heterogeneity of soil resources may have significant implications for community assembly and diversity. Plant diversity is positively correlated with soil heterogeneity (Fritter 1982; Rusch and Fernandez-Palacios 1995; Inouye and Tilman 1995), because resource heterogeneity promotes coexistence of plant species that sufficiently partition resources (Fritter 1982; Pacala and Tilman 1994). This suggests resource heterogeneity may exert a strong influence over the rate and direction of community assembly following disturbance (Baer et al. 2004).

A. tridentata plant communities provide an excellent opportunity to investigate the impacts of fire on microsite and herbaceous vegetation heterogeneity. These plant communities have pronounced differences in soil microsite and herbaceous vegetation characteristics between subcanopies and interspaces (Charley and West 1977; Doescher et al. 1984; Burke et al. 1987; Wight et al. 1992; Chambers 2001; Davies et al. 2007a), and experience periodic fires that remove *A. tridentata* (Wright and Bailey 1982). *A. tridentata* subcanopies generally provide more favorable microsites for plant growth and exhibit greater herbaceous vegetation cover, density, and biomass production than interspaces (Davies et al. 2007a). However, relatively little is known about the impact of fire on the characteristics of subcanopies and interspaces. A considerable amount of research has examined post-fire responses of herbaceous vegetation (Blaisdell 1953; Hedrick et al. 1966; Harniss and Murray 1973; Sneva 1972; Peek et al. 1979; Davies et al. 2007b) and soil nutrients at the community level (Hobbs and Schimel 1984; Blank et al. 1994; Young and Allen 1997; Davies et al. 2007b). A limited amount of research has evaluated hydrological characteristics and erosion in subcanopies and interspaces post-fire (Pierson et al. 2001; Ravi et al. 2007). Stubbs and Pyke (2005) and White et al. (2006) also measured inorganic and potentially mineralizable N concentrations, respectively, in subcanopies and interspaces after fire removed woody vegetation. However, information detailing the spatial arrangement of herbaceous vegetation and microsite characteristics in relation to subcanopies and interspaces after fire in woody-dominated plant communities is generally lacking.

The objective of this study was to determine the influence of fire on microsite and herbaceous vegetation spatial heterogeneity in woody vegetation [*A. tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh (Wyoming big sagebrush)]-dominated plant communities. We hypothesized that: (1) burning would decrease microsite and herbaceous vegetation spatial heterogeneity within the plant community; however, (2) burning would not completely eliminate resource island effects.

Materials and methods

Study sites

The study was conducted at the Northern Great Basin Experimental Range (NGBER), in southeastern Oregon (43°29′N, 119°43′W) about 56 km west of Burns, Oregon, USA. The regional climate is typical of the northern Great Basin with hot, dry summers and cool, wet winters. The NGBER receives on average 300 mm of precipitation annually. Crop-year precipitation (1 October–30 September) was 72 and 85% of the long-term average in 2002–2003 and 2003–2004, respectively. Six sites (blocks) with varying soils and herbaceous vegetation dominance, composition, cover, density, and biomass production were selected for the experiment. Elevation at the study sites is approximately 1,400 m above sea level and topography is flat (slopes <2°). Soils vary across the study area and include Haploxerolls, Agrixerolls, Durixerolls, and Durargids. *Artemisia tridentata* ssp. *wyomingensis* was the dominant shrub and *Achnatherum thurberianum* (Piper) Barkworth (Thurber’s needlegrass) or *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) was the dominant perennial bunchgrass depending on site. *Festuca idahoensis* Elmer (Idaho fescue), *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass), *Poa secunda* J. Presl (Sandberg bluegrass) and *Elymus elymoides* (Raf.) Swezey (squirreltail) were other common perennial bunchgrasses on the study sites. Prior to prescribed burning, the sites were determined to be late seral *A. tridentata* ssp. *wyomingensis*-dominated plant communities based on criteria in Davies et al. (2006). Tall perennial bunchgrasses dominated the understory and exotic annual grasses were only a minor component (<0.1% cover) of the plant communities. Prior to treatment, microsites and herbaceous vegetation varied between subcanopies and interspaces in each block. Microsite and herbaceous vegetation characteristics continued to vary between subcanopies and interspaces in the unburned portion of each block (Davies et al. 2007a). In general, subcanopies had greater herbaceous vegetation and more favorable microsite characteristics for plant growth compared to interspaces (Davies et al. 2007a).

Experimental design and statistical analysis

A randomized block design was used to compare intact subcanopies and interspaces to burned subcanopies and interspaces. Response variables were a variety of microsite and herbaceous vegetation characteristics. This design was also used to compare burned interspaces to burned subcanopies. Six sites were located across *A. tridentata* ssp. *wyomingensis*-bunchgrass dominated landscapes at the NGBER. At each site an 80 × 100-m (0.8 ha) block was selected for the experiment. One half of each block was randomly selected to be prescribed burned to remove *A. tridentata* ssp. *wyomingensis*. Treatments were designated as: subcanopies, interspaces, burned subcanopies, and burned interspaces. Sixty subcanopies and interspaces per block were randomly selected and marked with rebar prior to prescribed fall burning half of each block, which resulted in 30 subcanopies and interspaces in each half of each block. Prescribed burning occurred in early October 2002 and was applied as strip head-fires ignited with a gel-fuel terra torch (Firecon, Ontario, Oreg.). Burns were complete across the areas selected to be burned and removed all *A. tridentata* ssp. *wyomingensis* individuals. Wind speeds varied between 5 and 20 km h^{-1}, air temperatures were 10–25°C, and relative humidity (RH) varied from 10 to 35% during the prescribed burns. Moisture of fine fuels (herbaceous vegetation) were between 8 and 12% and fine fuel loads varied from 350 to 420 kg ha^{-1}. ANOVA was used to test for burned subcanopies and interspaces differences and differences between intact and burned locations in microsites and herbaceous vegetation variables that were not repeatedly sampled. Repeated-measures ANOVA was used for variables that involved repeated sampling (SAS Institute 2001). Between-subject effects were site and treatment. Within-subject effects were sampling date and the interactions of sampling date with between-subject effects. Fisher protected LSD was used to test for differences in means. Means were considered to differ at $P < 0.05$ ($\alpha = 0.05$). Intact and burned subcanopies and interspaces at all six sites were sampled in 2003 and 2004.

Measurements

Micro-environment

RH, air and soil temperature, and photosynthetically active radiation (PAR) measurements were recorded at 3-h intervals starting at midnight and ending at 9 p.m. each day from May up to and including early November in each treatment in every site. Soil temperature (°C) was measured and logged with Hobo four-channel temperature units at a depth of 4 cm below the soil surface. Two Hobo four-channel temperature units were placed at each site. Two channels from each unit recorded temperature for each location (subcanopy and interspace) and burned location (burned subcanopy and burned interspace). Air temperature (°C) and RH (%) were measured and logged at 30 cm above the soil surface with Hobo RH and temperature units. Six Hobo RH and temperature units were placed in each location and burned location in every site. PAR (μmol m^{-2} s^{-1}) was measured and logged with Hobo Microstations with smart sensors placed 10 cm above the soil surface. Four smart sensors measured PAR in each treatment in every site. For analysis, minimum and maximum temperatures and RH, and average PAR were determined for each day for each treatment in every site and then averaged for each month.

Soil characteristics

Soil water content was measured by collecting five soil cores from 0- to 15-cm and 15- to 30-cm depths at 2-week intervals from each treatment in every site during the growing season. Soil water content was determined gravimetrically by drying at 105°C until a constant weight was achieved. Soil pH, total C, total N, and organic matter in the upper 15 cm of the soil profile were determined from five soil samples, collected in July, from each treatment in every site. Total C and N were measured using a LECO CN 2000 (LECO, St. Joseph, Mich.). Organic matter was measured using an amended Rather method (Nelson and Sommers 1982). Soil NH_4^+ and NO_3^- content in the upper 15 cm of the soil profile were measured by collecting two samples from each treatment in every site every month during the growing season. Each sample consisted of five compiled 0- to 15-cm soil cores. N fractions were extracted using 2 N KCl solution. The extracted solution was analyzed for NO_3^- and NH_4^+ content by Oregon State University's Central Analytical Lab. Soil surface texture (0–15 cm) was determined by analyzing five samples from each treatment from each site using the hydrometer method (Gee and Bauder 1986).

Herbaceous

Herbaceous response variables measured were cover, biomass, density, photosynthetic rate, C isotope ratio ($^{13}C/^{12}C$) and N isotope ratio ($^{15}N/^{14}N$), and C and N concentrations. Herbaceous functional group biomass, cover by species, and perennial species densities were measured in thirty 0.4-m^2 (80 × 50 cm) sampling frames in each subcanopy, interspace, burned subcanopy, and burned interspace at each site. Mature *A. tridentata* ssp. *wyomingensis* subcanopies and interspaces were randomly selected and marked with rebar prior to burning. Herbaceous density and cover were measured in the two post-burn years, 2003 and 2004. Biomass production was measured in June 2004. Herbaceous vegetation was clipped by functional group, oven-dried, separated into current year's and previous years' growth, and weighed to determine biomass production.

Photosynthetic rates and nutrient concentrations were measured in *A. thurberianum* from each treatment to determine differences in the availability of resources to herbaceous vegetation. *A. thurberianum* was selected for sampling because it was common at every site, while other perennial bunchgrass species, though common to the study area, were not common at every site. Photosynthetic rates were determined for three *A. thurberianum* plants from each treatment at every site at 2-week intervals during the growing season using a LI 6200 portable photosynthesis unit and a LI 2100 leaf area meter (LI-COR, Lincoln, Neb.). C and N tissue concentrations and isotope ratios were measured from five *A. thurberianum* individuals from each treatment in every site. Samples were collected in late June, oven-dried, ground to pass through a 40-mesh screen, and then sent to the University of Utah Stable Isotope Research Facility for Environmental Research for analysis. The N isotope ratio was used to compare N availability. Because ^{15}N isotope discrimination increases with greater N availability, N isotope ratios can indicate relative N availability (Evans 2001). The C isotope ratio was used to compare water availability. The C isotope ratio can be used as a time-integrated estimate of water-use efficiency because heavier ^{13}C is discriminated against in C_3 plants (Farquhar et al. 1989; Ehleringer et al. 1993). Discrimination against ^{13}C increases with greater water availability (Toft et al. 1989).

Results

Micro-environment

The maximum daily soil temperatures varied between subcanopies and burned subcanopies ($P < 0.01$) and between burned subcanopies and burned interspaces ($P < 0.05$); however, they did not vary between interspaces and burned interspaces ($P = 0.09$) (Fig. 1). Burned subcanopies were on average 15.7 and 3.2°C warmer than subcanopies and burned interspaces, respectively. The minimum daily soil temperatures varied between subcanopies and burned subcanopies ($P < 0.01$); however, they did not vary between burned interspaces and burned subcanopies or between interspaces and burned interspaces ($P = 0.20$ and 0.31, respectively). The minimum daily soil temperatures in burned subcanopies were on average 3.4°C cooler than intact subcanopies. Maximum and minimum daily soil temperatures varied by sampling date ($P < 0.01$). The interactions between sampling date and treatments were not significant for maximum and minimum daily soil temperatures ($P > 0.05$).

Maximum and minimum daily air temperatures varied by sampling date ($P < 0.05$), but did not differ between treatments ($P > 0.05$). Average daily PAR for subcanopies was 300 μmol m^{-2} s^{-1} less than burned subcanopies from April to early November and varied by sampling date ($P < 0.01$). Average daily PAR did not vary between burned interspaces and burned subcanopies or between interspaces and burned interspaces, and the interactions between sampling date and treatments were not significant ($P > 0.05$). Maximum and minimum RH did not differ between treatments ($P > 0.05$); however, they varied by sampling date ($P < 0.05$).

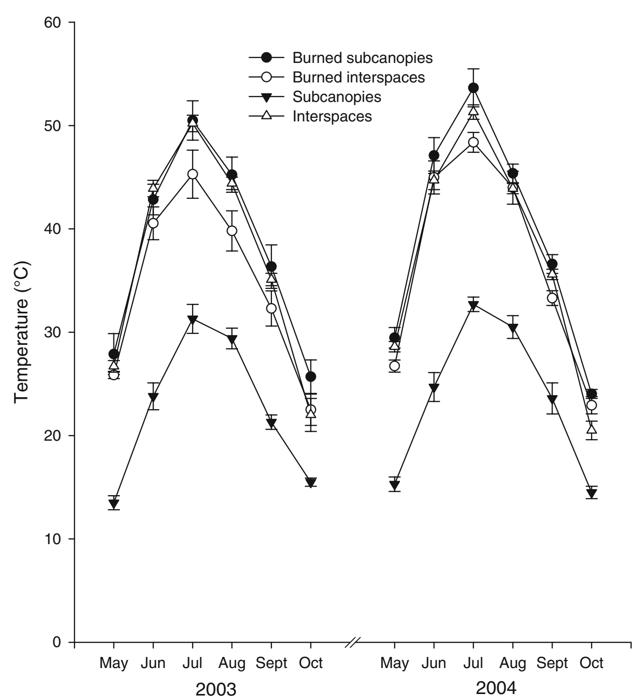

Fig. 1 Maximum daily soil temperatures (mean ± SE) at 4-cm depth in the subcanopies, interspaces, burned subcanopies, and burned interspaces

Soil characteristics

Percent sand, silt, and clay in the upper 15 cm of the soil profile did not differ between treatments or years ($P > 0.05$) (Table 1). Soil organic matter, pH, total C, and total N were greater in burned subcanopies than burned interspaces ($P < 0.05$) (Table 1). Soil organic matter, total C, and total N did not differ between subcanopies and burned subcanopies or between interspaces and burned interspaces ($P > 0.05$). Soil pH was higher in burned subcanopies than subcanopies ($P < 0.01$), but did not differ between interspaces and burned interspaces ($P = 0.24$). NO_3^- and NH_4^+ soil concentrations varied between burned subcanopies and burned interspaces ($P < 0.05$) (Fig. 2). Across the growing season burned subcanopies generally had greater NO_3^- and NH_4^+ concentrations than burned interspaces. Burned subcanopies also had greater NO_3^- and NH_4^+ concentrations than subcanopies ($P < 0.01$), but NO_3^- and NH_4^+ concentrations did not differ between interspaces and burned interspaces ($P > 0.05$). NO_3^- and NH_4^+ soil concentrations also varied by sampling date ($P < 0.05$). NO_3^- and NH_4^+ concentrations response to burned subcanopies and burned interspaces did not vary by sampling date ($P > 0.05$). NO_3^- concentrations response to subcanopies and interspaces compared to burned subcanopies and burned interspaces varied by sampling date ($P < 0.05$), but NH_4^+ concentrations did not ($P > 0.05$).

Soil water content (0–15 cm) varied by sampling date ($P < 0.01$), but did not differ between burned subcanopies and burned interspaces, between interspaces and burned interspaces, or between subcanopies and burned subcanopies ($P > 0.05$) (Fig. 3). The interaction between sampling date and burned location was also not significant ($P = 0.14$). Soil water content in subcanopies and interspaces compared to burned subcanopies and burned interspaces varied by sampling date ($P < 0.05$). Soil water content (15–30 cm) did not vary between burned subcanopies and burned interspaces, between interspaces and burned interspaces, or between subcanopies and burned subcanopies ($P > 0.05$). Soil water content (15–30 cm) varied by the response of burned subcanopies and burned interspaces to sampling date ($P = 0.04$). Soil water content also varied by the response to sampling date of interspaces compared to burned interspaces ($P = 0.05$).

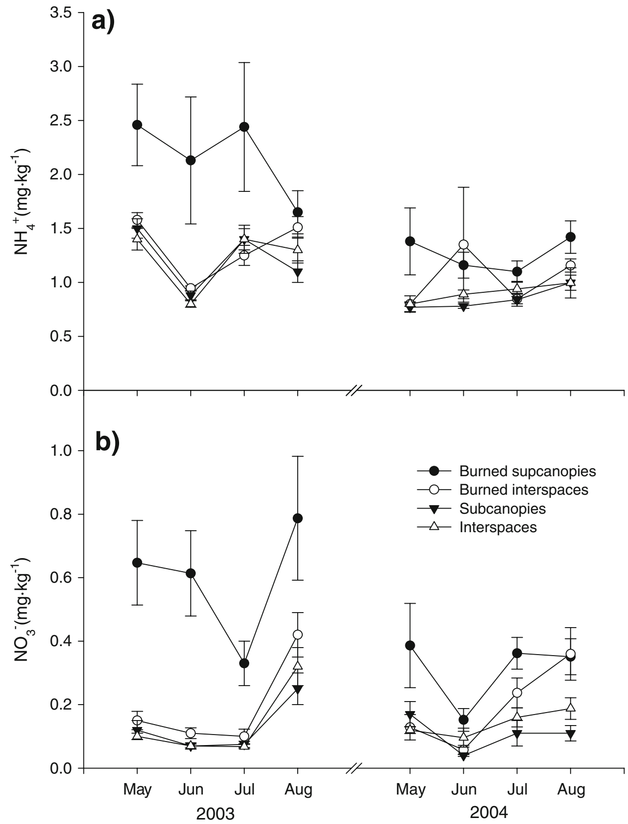

Fig. 2 Soil NH_4^+ (**a**) and NO_3^- (**b**) concentrations (mean ± SE) in the subcanopies, interspaces, burned subcanopies, and burned interspaces

Table 1 Soil characteristics (0–15 cm) in the subcanopies, interspaces, burned subcanopies, and burned interspaces

Soil parameter	Subcanopies (mean)	Interspaces (mean)	Burned subcanopies (mean)	Burned interspaces (mean)	Significance for difference of means
Clay (%)	7	8	7	8	NS
Silt (%)	23	24	23	24	NS
Sand (%)	70	68	70	68	NS
pH	7.1	6.9	7.3	6.9	a, b
Organic matter (%)	1.43	1.30	1.35	1.20	a
Total C (%)	0.99	0.76	0.96	0.74	a
Total N (%)	0.08	0.07	0.08	0.07	a

NS Differences were non-significant for all comparisons ($P > 0.05$)

[a] Significant differences between burned subcanopies and burned interspaces ($P < 0.05$)

[b] Significant differences between subcanopies and burned subcanopies ($P < 0.05$)

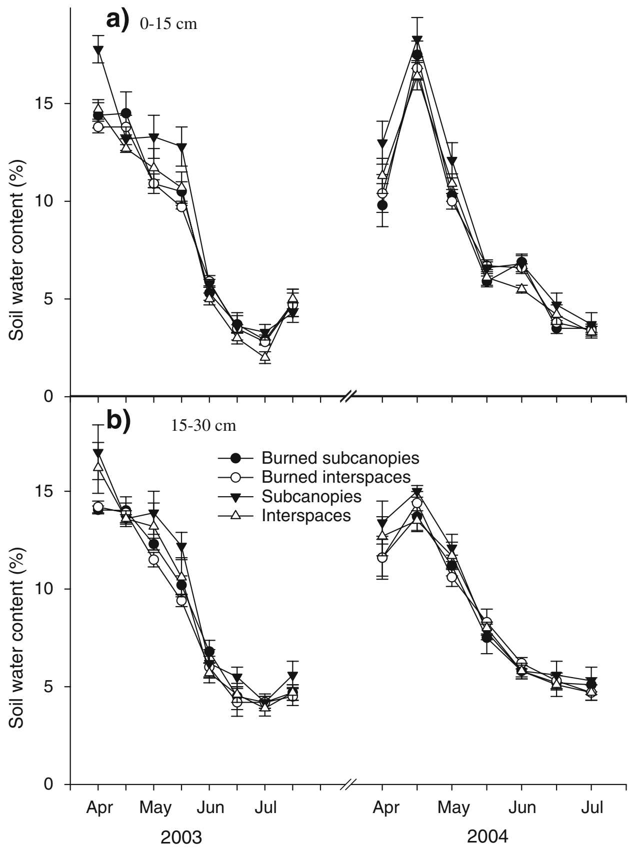

Fig. 3 Soil water content (mean ± SE) in the subcanopies, interspaces, burned subcanopies, and burned interspaces at 0- to 15-cm (**a**) and 15- to 30-cm (**b**) depths

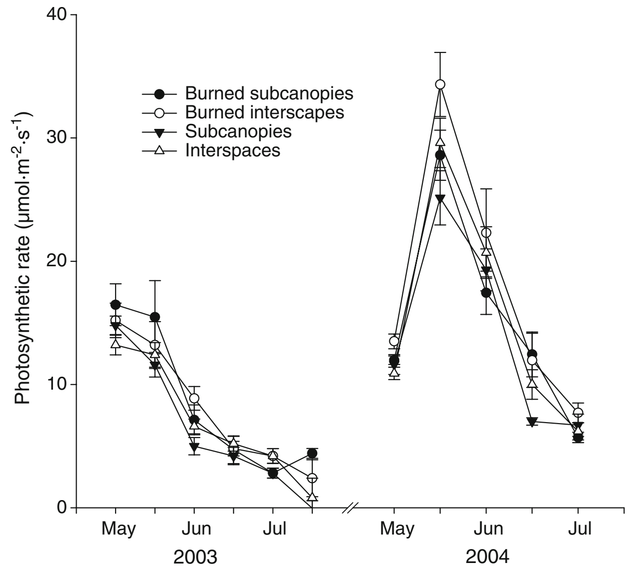

Fig. 4 Photosynthetic rates (mean ± SE) for *Achnatherum thurberianum* in the subcanopies, interspaces, burned subcanopies, and burned interspaces

Vegetation

Physiological response of A. thurberianum

A. thurberianum C and N isotope ratios did not differ among burned subcanopies and burned interspaces ($P > 0.05$) (Table 2), but differed between 2003 and 2004 ($P < 0.01$). *A. thurberianum* C and N isotope ratios did not differ between interspaces and burned interspaces ($P > 0.05$). N isotope ratios were greater in subcanopies than burned subcanopies ($P = 0.01$), but C isotope ratios did not differ between subcanopies and burned subcanopies ($P = 0.06$). Total percent C and N of *A. thurberianum* did not differ between burned subcanopies and burned interspaces, between interspaces and burned interspaces, or between subcanopies and burned subcanopies ($P > 0.05$). Total percent C and N varied by year ($P \leq 0.01$).

Photosynthetic rates of *A. thurberianum* also did not vary between burned subcanopies and burned interspaces, between interspaces and burned interspaces, or between subcanopies and burned subcanopies ($P > 0.05$). Photosynthetic rates varied by sampling date, generally declining over the growing season ($P < 0.01$) (Fig. 4).

Herbaceous cover, density, and biomass production

Tall tussock perennial grass, *P. secunda*, perennial forb, annual grass, annual forb, total herbaceous, litter, and moss

Table 2 C and N characteristics of *Achnatherum thurberianum* in the subcanopies, interspaces, burned subcanopies, and burned interspaces

Characteristic	Subcanopies (mean)	Interspaces (mean)	Burned subcanopies (mean)	Burned interspaces (mean)	Significance for difference of means
$^{13}C/^{12}C$ ratio (‰)	−26.6	−26.1	−26.3	−26.1	NS
$^{15}N/^{14}N$ ratio (‰)	2.6	2.8	2.0	2.2	[a]
Total C (%)	42.0	42.1	41.9	42.7	NS
Total N (%)	1.3	1.2	1.1	1.1	NS

NS Differences were non-significant for all comparisons ($P > 0.05$)

[a] Significant differences between subcanopies and burned subcanopies ($P < 0.05$)

cover and bare ground did not differ between burned subcanopies and burned interspaces ($P > 0.05$) (Fig. 5). Tall tussock perennial grass, *P. secunda*, annual grass, litter, and moss cover were greater in subcanopies than burned subcanopies ($P < 0.05$). Bare ground was less in subcanopies than burned subcanopies ($P < 0.01$) and perennial forb, annual forb, and total herbaceous cover did not differ between subcanopies and burned subcanopies ($P > 0.05$). Litter and *P. secunda* cover were greater in interspaces than burned interspaces ($P < 0.05$), but tall tussock perennial grass, annual grass, perennial forb, bare ground, total herbaceous, and moss cover did not differ between interspaces and burned interspaces ($P > 0.05$).

Tall tussock perennial grass and total perennial grass (tall tussock perennial grass and *P. secunda*) densities were greater in burned subcanopies than burned interspaces ($P = 0.04$ and 0.03, respectively) (Fig. 6). *P. secunda* density did not differ between burned subcanopies and burned interspaces ($P = 0.05$). Tall tussock perennial grass, total perennial grass, and *P. secunda* densities did not differ between subcanopies and burned subcanopies or between interspaces and burned interspaces ($P > 0.05$).

Herbaceous functional groups and total herbaceous biomass production did not differ between burned subcanopies and burned interspaces ($P > 0.05$) (Fig. 7). Annual grass and *P. secunda* biomass production was greater in subcanopies than burned subcanopies and tall tussock perennial grass and perennial forb biomass production was less in subcanopies than burned subcanopies ($P < 0.05$). Annual grass and *P. secunda* biomass production was greater in interspaces than burned interspaces and perennial forb and tall tussock perennial grass biomass production was less in interspaces than burned interspaces ($P < 0.05$).

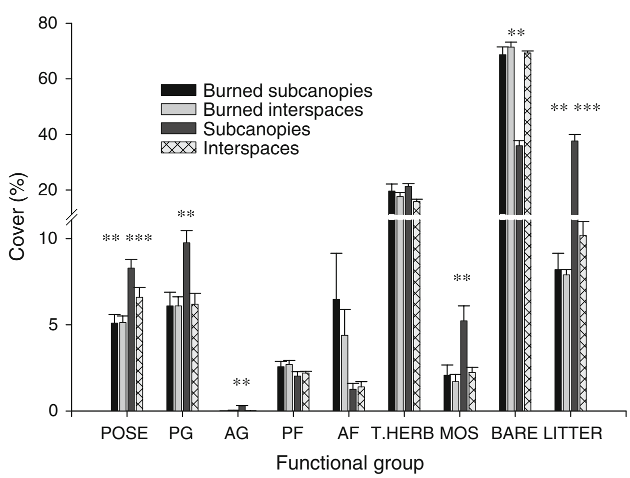

Fig. 5 Subcanopies, interspaces, burned subcanopies, and burned interspaces functional group cover values (mean + SE). *Double asterisk* indicates significant differences between subcanopies and burned subcanopies ($P < 0.05$), *triple asterisk* indicates significant differences between interspaces and burned interspaces ($P < 0.05$). *PG* Tall tussock perennial grass, *POSE Poa secunda*, *PF* perennial forb, *AG* annual grass, *AF* annual forb, *BARE* bare ground, *T.HERB* total herbaceous

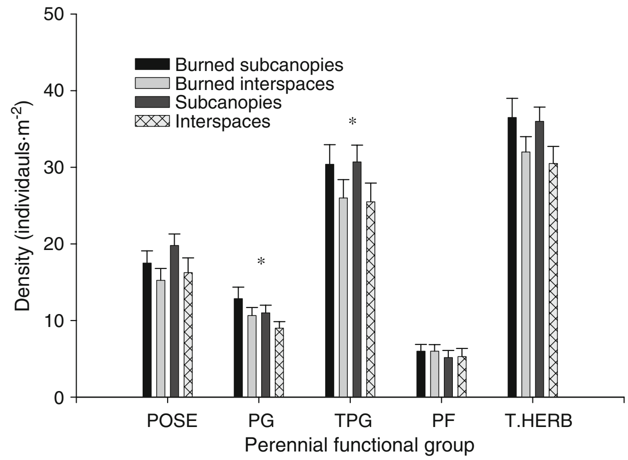

Fig. 6 Perennial functional group density values (mean + SE) in the subcanopies, interspaces, burned subcanopies, and burned interspaces. *Single asterisk* indicates significant differences between burned subcanopies and burned interspaces ($P < 0.05$). *TPG* Total perennial grass (PG + POSE); for other abbreviations, see Fig. 5

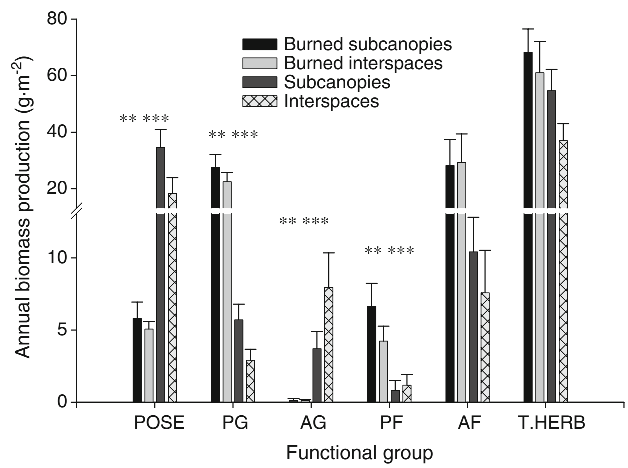

Fig. 7 Functional group annual biomass production (mean ± SE) in the subcanopies, interspaces, burned subcanopies, and burned interspaces. *Double asterisk* indicates significant differences between subcanopies and burned subcanopies ($P < 0.05$), *triple asterisk* indicates significant differences between interspaces and burned interspaces ($P < 0.05$). For abbreviations see Fig. 5

Discussion

Burning appeared to reduce the influence of resource islands on herbaceous vegetation within woody plant-dominated communities. Prescribed burning of *A. tridentata* ssp. *wyomingensis*-bunchgrass communities decreased microsite and herbaceous vegetation heterogeneity within a stand. The structural diversity created by *A. tridentata* ssp. *wyomingensis* canopies was removed with burning.

However, burning did not completely eliminate the heterogeneity of resource concentrations created by *A. tridentata* ssp. *wyomingensis*.

Burning eliminated or greatly reduced micro-environmental differences between subcanopies and interspaces. The moderating effect of the subcanopy on soil temperatures reported by Davies et al. (2007a) was reversed with prescribed burning. In contrast to lower soil maximum temperatures in intact subcanopies compared to intact interspaces (Pierson and Wight 1991; Davies et al. 2007a), soil maximum temperatures were greater in burned subcanopies compared to burned interspaces. Prescribed burning resulted in burned subcanopies and burned interspaces being more similar in soil temperatures than intact subcanopies and interspaces. Burned interspaces and burned subcanopies also generally did not differ in soil water content, which is dissimilar to the greater soil water content in intact subcanopies than intact interspaces reported by Wight et al. (1992), Chambers (2001) and Davies et al. (2007a). This general lack of micro-environmental differences between burned subcanopies and interspaces is probably due to the loss of the structural component provided by *A. tridentata* ssp. *wyomingensis* canopies. The shade provided by *A. tridentata* ssp. *wyomingensis* canopies probably moderated soil temperatures and reduced evapotranspiration (Davies et al. 2007a). Increased solar radiation results in warmer temperatures (McCune and Keon 2002), which would also increase evapotranspiration. Thus, the increase in solar radiation in subcanopies following prescribed burning probably reduced other micro-environmental differences between burned subcanopies and burned interspaces.

However, *A. tridentata* ssp. *wyomingensis* subcanopy and interspace microsites maintained some differences after burning. Soil resource differences were common after burning, while micro-environmental differences were often lacking. The greater soil resources in burned subcanopies compared to burned interspaces were similar to differences in undisturbed communities reported by Charley and West (1977), Doescher et al. (1984), Burke et al. (1987), and Davies et al. (2007a). The increase in inorganic N in burned subcanopies was similar to the results reported by Stubbs and Pyke (2005). However, microsites may have differed between burned subcanopies and burned interspaces because the impacts of prescribed burning varied between subcanopies and interspaces. For example, prescribe burning increased soil inorganic N concentrations in subcanopies, while inorganic N concentrations did not differ between interspaces and burned interspaces.

Although greater inorganic soil N concentrations in burned subcanopies compared to burned interspaces suggest that N was more available to herbaceous plants growing in burned subcanopies than burned interspaces, the lack of a difference in N isotope ratios of *A. thurberianum* from burned subcanopies and burned interspaces suggest that N availability to plants may not have differed between burned subcanopies and burned interspaces. Plant N isotope ratios are expected to increase as N becomes more available (Evans 2001). Burned subcanopies and burned interspaces did not differ in C and N isotope ratios, photosynthetic rates, and herbaceous biomass production suggesting that, in general, resource availability was similar. The lack of physiological response of *A. thurberianum* to burned subcanopies and interspaces is similar to Davies et al. (2007a) results for intact subcanopies and interspaces, except in that study C isotope ratios varied between intact subcanopies and interspaces.

Herbaceous vegetation characteristics differed between intact and burned locations, suggesting that burning alters the spatial heterogeneity of herbaceous vegetation created by woody vegetation. Prescribed burning had varying effects on herbaceous vegetation production and cover depending on functional group and location. Similarly, Davies et al. (2007b) reported varying effects of prescribed burning on different functional groups at the community level. The general lack of differences in herbaceous vegetation between burned subcanopies and burned interspaces compared to differences between subcanopies and interspaces reported by Davies et al. (2007a) can largely be explained by the impacts of prescribed burning on microsite characteristics. The lack of differences in herbaceous vegetation production and cover between burned subcanopies and burned interspaces is probably due to lack of significant differences in soil temperatures and water content. Davies et al. (2007a) reported that herbaceous vegetation production and cover were probably greater in subcanopies compared to interspaces because soil temperatures were moderated and soil water content was higher in subcanopies than interspaces. The heterogeneity in herbaceous vegetation characteristics was largely eliminated with burning; except that perennial herbaceous density differences remained.

Tall tussock perennial grass and total perennial grass densities were greater in burned subcanopies than burned interspaces. However, none of the perennial vegetation densities varied when comparing intact to burned locations. This suggests that density differences between subcanopies and interspaces were maintained after burning, because prescribed burning resulted in limited mortality of perennial herbaceous vegetation. Davies et al. (2007b) and Davies and Bates (2008) reported limited mortality of perennial herbaceous vegetation when prescribed fall burning was applied in *A. tridentata* ssp. *wyomingensis*-bunchgrass communities. Thus, density differences between burned subcanopies and burned interspaces were probably an artifact of prior densities and not the result of significant differences in resource availability to herbaceous vegetation.

Our results demonstrate that burning alters microsite and herbaceous vegetation characteristics of subcanopies and interspaces. Ours results also suggest that burning increases the similarity between subcanopies and interspaces. Some microsite differences remain after prescribed burning removed *A. tridentata* ssp. *wyomingensis*, but appear to have little effect on herbaceous vegetation. Thus, disturbances that remove the woody vegetation that is creating resource islands and facilitating other vegetation growth appear to decrease the heterogeneity of herbaceous vegetation and microsite characteristics within these plant communities. This supports speculation by Ravi et al. (2007) that fire could decrease the resource heterogeneity created by shrubs in arid ecosystems. Alterations to resource spatial patterns in ecosystems with woody plant encroachment (Hibbard et al. 2001) may have the potential to be reversed or at least be reduced with burning. Repeated burning may even further increase the homogeneity between burned subcanopies and burned interspaces. White et al. (2006) reported that after two burns potentially mineralizable N was not different between soils under shrubs and grasses, but differences remained under shrubs compared to bare areas. Our results suggest that even one burn will reduce the spatial heterogeneity of resources and subsequently increase the homogeneity of herbaceous vegetation.

Conclusion

Burning appears to largely eliminate micro-environmental differences between subcanopies and interspaces and thus, decreases herbaceous vegetation heterogeneity within plant communities. However, burned subcanopies and burned interspaces differed in soil resources, which may promote heterogeneity of vegetation composition and productivity over time. Burning does not eliminate the resource island, but may reduce its affects on herbaceous vegetation. However, seedling establishment may vary between burned subcanopies and burned interspaces due to the difference in soil resources. Rusch and Fernandez-Palacios (1995) reported that spatial heterogeneity of soil resources influenced seedling success in grasslands. The difference in soil resources between burned subcanopies and burned interspaces also suggests that the invasibility of plant communities may vary between microsites after fire. Coexistence and diversity, which can include exotic species, are promoted by heterogeneity of resources (Fritter 1982; Pacala and Tilman 1994; Rusch and Fernandez-Palacios 1995; Inouye and Tilman 1995). The influence resource islands have on seedling establishment and invasibility after disturbance needs to be investigated to better understand plant community dynamics. Results of this study suggest that the influence of disturbances on herbaceous vegetation in woody vegetation dominated plant communities varies between subcanopies and interspaces. This study demonstrates the importance of woody vegetation to heterogeneity in plant communities and that resource islands exist even after disturbances have removed the woody vegetation, which probably influences diversity and community assembly.

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